Tooth Diversity

Although the evolution of tooth structure seems highly conserved, remarkable diversity exists among species due to different living environments and survival requirements. Along with the conservation, this diversity of evolution allows for the optimized structures and functions of teeth under various service conditions, providing valuable resources for the rational design of biomimetic materials.

1. Mammal Teeth

1.1. Human Teeth

Enamel

Enamel, the hardest material in the human body, consists of 96% hydroxyapatite (HAP) and 4% water and proteins, mainly amelogenin and enamelin. It constitutes the outermost layer of teeth with a thickness up to several mm [1], forming a barrier to protect teeth from external physical and chemical damage. Enamel has a hardness of 5.00 ± 0.22 GPa [2], a modulus of 97.12 ± 2.95 GPa [2], and a fracture toughness of 0.67 ± 0.12 MPa $m^{1/2}$ [3], much higher than that of pure HAP of 0.3 MPa $m^{1/2}$ [4]. The superior fracture tolerance of enamel is mainly attributed to its hierarchical structure [5][6]. The crystal first forms mineral nanofibers (30–40 nm), which gather into fiber bundles (80–130 nm) and then assemble into prisms (6–8 µm) [6]. Human enamel is characterized by the predominance of key-hole-shaped prisms among different Boyde's patterns [7]. These prisms are assembled into strips, which are arranged differently across the thickness of enamel layer, defining enamel types. On the occlusal surface, prismless enamel may also exist [7]. In the outer enamel, the prisms are almost parallel to each other as radial enamel. However, in the inner enamel, prisms are cross arranged, forming decussating enamel. There are two characteristic areas in the inner enamel, namely the para-zone (P-zone) and the dia-zone (D-zone), according to the orientation of bands of prisms sectioned relative to their long axes [8], corresponding to the well-developed Hunter–Schreger bands [9][10]. Surrounding the prisms is interprismatic enamel. In interprismatic enamel, which is distinct from crystallites within prisms that are oriented roughly parallel to the prism long axis, the crystallites fan out from the center toward the edges. The boundaries between prismatic and interprismatic enamels appear as distinct structures as protein sheaths. At the next level, *schmelzmuster* comprises different enamel types based on their arrangement. Dentition is the highest hierarchical level, referring to the variation of *schmelzmuster* from tooth to tooth.

The change of the spatial organization of prisms from the occlusal surface to the dentin-enamel junction (DEJ) is accompanied by the gradual reduction of densities [11][12]. The main inorganic compounds of human enamel are calcium, phosphate, carbonate, magnesium, and sodium. The mass percentage of CaO and P_2O_5 decreases from the enamel surface to the dentin, whereas Na_2O and MgO increases [13]. It has been shown that the highest content of Ca and P may be related to the largest values of hardness and modulus at the enamel surface. Na and Mg are mainly present in amorphous interphase (AIP) around organic proteins, so the content of Na and Mg is the highest near dentin. The presence of organic proteins and Na and Mg increases the fracture toughness of enamel, which is a function of the distance between dentin and enamel. Mg-calcium phosphate is the main phase of AIP at the grain boundary for strengthening the interfacial connections between mineral nanofibers and improving energy dissipation [14].

Dentin and the Dentin–Enamel Junction (DEJ)

Different from enamel, the sensitive and soft dentin forms throughout life. The 5 nm thick HAP crystallites in the collagen fibril scaffold are much less aligned in dentin. It consists of 70% HAP, 20% organics, and 10% water, with a modulus of 21.1 ± 1.3 GPa, a hardness of 0.51 ± 0.02 GPa [15], and a toughness of 1–3 MPa $m^{1/2}$ [16]. These properties are necessary for the support of hard enamel and enable teeth to withstand lifelong masticatory stress. The distinctive cylindrical dentine tubules have the highest density near the pulp and the lowest near the enamel, and the diameter

gradually decreases from the pulp to the dentin-enamel junction (DEJ) [17]. Structural overlap at the DEJ is critical to the survival of this wavy interface because it allows the stress on the tooth surface to gradually dissipate into the dentin, rather than acting as a barrier. This coupling results in a gradual change of hardness observed in this area, from ca. 4 GPa on the enamel side to ca. 1 GPa on the dentin side [17]. The gradient structure of DEJ region ensures the stress distribution and the prevention of possible microcracks.

1.2. Other Mammal Teeth

Teeth from other primates also mostly consist of prismless enamel, radial enamel, and decussating enamel from the occlusal surface to the DEJ, although decussating enamel may be absent in small primates [7]. Teeth from other mammals such as the panda premolar [18], wild wolf fangs [19], bovine teeth [20], wild boar tusks [21], and canine posterior molars [22] are all composed an inner dentin layer, an enamel layer, and the DEJ. This layered configuration balances the anti-abrasive properties and fracture resistance of various types of teeth. For example, the modulus and hardness of sheep molar enamel are both lower than that of human enamel, but sheep enamel is approximately 30% more resistant to wear [23].

The main biominerals of mammal teeth are HAP, but Interspecific variations in enamel crystallite compositions, sizes, and shapes are commonly observed [24]. Among human, ovine, porcine, and bovine teeth, porcine enamel has the highest content of organic matter, whereas human enamel has the lowest content. The less presence of organic matter, the larger the crystallite size, as found in human enamel [24]. Compared with the relatively small variations of crystallite sizes among these animals, twinned crystallites as thick as 500 nm were found in wild boar tusks [21], which are much thicker than the fiber of 35 nm in panda teeth [18]. Regarding the shape, although enamel crystallites are all elongated, their cross-sections are hexagonal and rhomboidal [7] or even circular [25]. An interesting case is found for colored enamel in rodent animals. AIP consists of iron compounds and amorphous calcium iron phosphate, which makes AIP harder and more acid resistant [26].

More diversity can be found in the next hierarchical level: enamel type. The first difference is evidenced in the relative orientation of interprismatic crystallites to the prisms. Although rod decussation exists in both human and pig enamel, there is a decussation plane between rod and interrod crystallites in pig enamel [27]. This decussation plane is formed due to the high angles between prismatic and interprismatic crystallites, which are arranged as sheets to partition the enamel rods. In contrast, the orientation of interprismatic crystallites in human radial enamel deviates only slightly from the long axis of prismatic crystallites. The additional decussation plane makes pig enamel less resistant to horizontal tensile stresses but enables more efficient arrest of crack propagation in multiple directions. Similar difference was found from the occlusal surface of enamel from canine and bovine [22]. The interprismatic crystallites in canine enamel are only slightly inclined to the prisms; however, in bovine enamel, they are nearly perpendicular to each other [22]. This modified type of radial enamel is also found in wild boar tusks [21] but is absent in panda teeth [18][28].

Hunter–Schreger bands (HSB) packing densities increase with loadings and are the highest in areas with concentrated stress, such as the occlusal surfaces of posterior teeth and the incisal regions of incisors [10]. The HSB packing density of otter enamel is 19.4 HSB mm^{-1}, in contrast to 14 HSB mm^{-1} in human enamel, contributing to the 2.5 times higher toughness of the former [25]. Considerable interspecific variations in HSB can be found in some bone-feeding carnivora, such as extant hyenas [29]. Distinct from the normal undulating horizontal HSB, adjacent zigzag HSB are joined by vertical decussating prism bundles, which radiate outward from the central axis of the tooth when viewed from the transverse section. The structure resists fracture under stresses from different directions and represents an adaption to withstand remarkably high stresses during occlusion, a specialization for bone-eating.

To adapt to feeding habits, the tooth size, enamel thickness, and cuspal morphologies of mammals also vary toward optimized load-bearing abilities. Cattle need to chew for a long time, about 10 h a day, and the broad enamel certainly needs good wear and fatigue resistance. Bone-feeding carnivores, however, need much greater bite forces from teeth, which are, therefore, much sharper than cattle teeth. Studies have also shown that among primates, morphological variations may play a more important role in the different load-bearing abilities of molar teeth than materials properties such as modulus and hardness [30].

2. Aquatic Animal Teeth

2.1. Fluorapatite Teeth

Shark Enameloid

Shark teeth are produced and discarded tens of thousands of times during the lifetime of a shark [31]. Distinct from human enamel, shark tooth enameloid consists mainly of fluorapatite (FAP) with a minor amount of collagen. The 5–6% content of fluoride ions in the crystal lattice ensures a better protection effect against acid [32]. Although FAP is harder than HAP, the modulus and hardness of shark teeth and human teeth is comparable both for dentin and enameloid/enamel [33]. A comparison of the tearing teeth of *Isurus oxyrinchus* with the cutting teeth of *Galeocerdo cuvier* showed that the different biological functions of shark teeth are mainly controlled by their geometry [33], a common factor for maximizing the bite forces in the teeth of piranha [34], black drum fish [35], and black carp [36]. *Isurus oxyrinchus* enameloid has FAP crystallites that are 50–80 nm thin and more than 1 μm long [37]. Underneath the shiny layer at the surface, where the crystallites are randomly oriented, there are circumferential bundles, radial bundles, and axial bundles down to the dentin. The size of radial bundles decreases from the dentin–enameloid junction towards the distal layers of the enameloid, where they proceed between the circumferential bundles and project into the superficial shiny layer. Similar to *Isurus oxyrinchus* and *Galeocerdo cuvier*, most other shark teeth also have a superficial shiny layer and an inner layer consisting of crystallite bundles with changing degrees of structural organization from distal to proximal. However, there are some exceptions. The shiny layer of enameloid is absent in the teeth of *Carcharhinus plumbeus*, and in some species, the bundled layer is replaced by thick dentin [38].

In the grasping teeth of the Port Jackson shark, a graded alignment of FAP crystallites in the cusp was observed [39]. The FAP crystallites in the outer enameloid are aligned and parallel to the surface and gradually transition into a tangled organization in the inner enameloid. The graded architecture provokes a location-specific damage response for a mechanism of shape preservation. A crack-guiding effect promotes the circumferential chipping damage in the outer enameloid, whereas a crack deflection strategy slows erosion by dissipating energy in the inner enameloid.

Parrotfish Enameloid

FAP as the main tooth component also prevails in many other fish species, such as parrotfish. The enameloid of *Chlorurus microrhinos* is even stiffer than that of shark teeth [40], consisting of 100 nm wide, micrometer-long FAP crystals co-oriented and assembled into interwoven bundles. These fibers gradually decrease in average diameters from ca. 5 μm at the back to ca. 2 μm at the tooth tip, which corresponds to the gradient in modulus and hardness. The modulus is 124 ± 8 GPa, and the hardness is 7.3 ± 0.5 GPa near the biting surface. The individual tooth exhibits a quasi-plastic contact response with a high indentation yield strength of ca. 6 GPa, resulting in extremely high abrasion resistance. The nanoscale structure and the interwoven fibers contribute to the high toughness of ca. 2.5 MPa m$^{1/2}$.

Black Drum Fish Enameloid

The black drum fish (*Pogonias cromis*) enameloid is the stiffest reported so far, reaching a modulus of 126.9 ± 16.3 GPa and a hardness of 5.0 ± 1.4 GPa [35]. This is attributed to the stiffening effect of Zn and F doping in apatite crystals and the preferential co-alignment of crystallographic c-axes and enameloid rods along the biting direction. In the inner enameloid region, the apatite crystals are arranged into intertwisted rods with crystallographic misorientation for increased crack resistance and toughness. The high fracture toughness of ca. 1.12 MPa m$^{1/2}$ of the outer enameloid also promotes local yielding instead of fracture during crushing contact with mollusk shells. Similar with the teeth of parrotfish, the diameters of enameloid rods decrease from the dentin–enameloid junction to the outer surface.

Crayfish Mandible

An unusual, crystalline enamel-like FAP layer was found in the mandibles of the arthropod *Cherax quadricarinatus* (freshwater crayfish) [41]. Similar to most other tooth structures, crayfish teeth also have three elements: a hard covering, a soft support, and a hierarchical interface between these layers. Amorphous calcium carbonate, amorphous calcium phosphate, calcite, and fluorapatite all coexist in well-defined functional layers in proximity within the mandible.

2.2. Self-Sharpening Teeth

Calcite Teeth in Sea Urchin

Self-sharpening teeth of sea urchin are made of calcite. They rely on chipping to maintain shape edges; however, the tooth grows continuously and moves out to the front from its base. The teeth of California purple sea urchin, *Strongylocentrotus purpuratus*, are made of calcite plates, fibers, and the polycrystalline matrix between them. The polycrystalline matrix comprises 10 to 20 nm nanoparticles of Mg-calcite [42][43]. There are organic layers surrounding plates and fibers that behave as the "fault lines" in the tooth structure [44]. Shedding of tooth components at these discontinuities exposes the robust central part of the tooth, "the stone", which becomes the grinding tip. The central stone part is comprised of Mg-rich polycrystalline matrix nanoparticles, and narrower fibers than those in the lateral side. These

small fibers run roughly parallel to the length of the stone part [45]. An in situ wear test also confirmed that the structural geometry and chemical makeup of the tooth components are the key for maintaining sharp tips [46].

Iron Oxide Teeth in Chiton and Limpet

The chiton teeth are also self-sharpening, as enabled by a similar mechanism of breaking at pre-determined locations [47]. The region close to the anterior surface of the tooth cusp of *Acanthochiton rubrolineatus* has a microstructure oriented parallel to the abrasive surface with an average hardness of Hv270, whereas the underneath area has a microstructure oriented perpendicular to the abrasive surface with an average hardness of Hv490. The different abrasive property of two regions results in the faster wear down of the anterior surface than the underneath area so that the tooth keeps a sharp cutting edge under the characteristic grazing action. Chiton tooth caps from *Cryptochiton stelleri.* are three times harder than human enamel and are the hardest biominerals investigated so far (9–12 GPa) [48]. The main reason is that chiton teeth are covered in magnetite, a harder biomineral than HAP and FAP [49]. Chiton teeth also achieve impressive mechanical properties through a layered composite structure, which consists of a hard shell of organically wrapped and highly oriented nanostructured magnetite rods surrounding a soft core rich in organic iron phosphate [50]. The core–shell structure, which is hard on the outside and soft on the inside, provides strong cushioning and shock absorption. The magnetite and chitin fibers support each other in different directions to make the teeth less likely to bend and break. The regular internal structure inhibits crack formation, and even when cracks do form, they spread along the gaps between the structural units, preventing the entire tooth from collapsing. Another example of iron oxide teeth is from limpet [51]. The highest recorded tensile strength (3.0 to 6.5 GPa) of limpet teeth among biological materials is attributed to a high mineral volume fraction of reinforcing goethite nanofibers with diameters below a defect-controlled critical size, which are aligned with chitin matrix.

2.3. Transparent Teeth

An Invisible Weapon for Dragonfish

Although the main function of teeth is concerned with mechanical properties, the deep-sea dragonfish, *Aristostomias scintillans*, has evolved transparent teeth that are invisible under bioluminescence, showing no contrast to the surrounding water [52]. The high transparency is a unique property that is the result of the nanoscale texture of teeth. The enamel-like layer is highly mineralized, consisting of amorphous/nanocrystalline HAP (ca. 20 nm grain size), whereas the dentin consists of an array of interpenetrating nanorods (ca. 5 nm in diameter) of HAP embedded within a collagen matrix. Furthermore, dragonfish teeth are also sufficiently thin (ca. 60 μm) and lack microscale features such as dentin tubules, effectively reducing Rayleigh scattering. The importance of the transparent array of hard sharp teeth may be related to camouflage. The adaptation to thriving in the aphotic zone produces a deadly invisible weapon for dragonfish.

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